Posture and pauses during parturition in flying-foxes (Genus *Pteropus*, suborder Megachiroptera)

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ABSTRACT

Observations of births in wild and captive *Pteropus* confirm that the usual birthing posture of the mother is hanging from the hind-legs, and not, as was asserted in a recent report, hanging by the thumbs. Observations of births in wild and captive *Pteropus* show that after emergence of the neonate's head, it is not unusual for the birth-process to be interrupted by a resting period of a few minutes to several hours. The final stages of birth are then completed relatively rapidly and usually without the need for intervention. Factors underlying this pause in parturition are discussed.

Key words: Parturition, Posture, Flying-fox.

INTRODUCTION

I have elsewhere (Martin 1998) emphasized that, in caring for animals we should attempt to meet their *evolved needs*, and not impose arbitrary and inappropriate regimens, or unnecessary interventions. To meet this aim, it is essential that animal carers have an accurate knowledge of the normal processes. I was dismayed therefore, to find misconceptions being promulgated in the literature, concerning parturition (the birth-process) in *Pteropus* flying-foxes, with descriptions and assertions which were incompatible with observations made in the wild, and in successful captive breeding colonies of *Pteropus poliocephalus*, *P. alecto* and *P. scapulatus* over the last decade or so (Martin, Kennedy, Little, Luckhoff, O'Brien, Pow, Towers, Waldon and Wang 1995).

THE POSTURE OF *PTEROPUS* DURING PARTURITION

A paper by Kunz, Allgaier, Seyjagat and Caligiuri (1994) described a single breech-birth in *P. rodricensis* (The Rodrigues Flying-fox) in which, during labour, the female repeatedly went into a position whereby she hung head-up by the thumbs, and which was described by the authors as,

"the feet-down birthing posture".

The female adopted this posture on five occasions; on the first she did so alone, subsequently, she did so after a "helper" female had taken up the posture immediately in front of her. The authors interpreted this as the attending female,

" 'tutoring' her in a feet-down birthing posture"

This posture, beautifully illustrated in Kunz *et al.* (1994), is identical with that characteristically adopted reflexly for defaecation-and-urination in the Australian flying-foxes, *Pteropus poliocephalus*, *P. alecto* and *P. scapulatus*. I have also observed it adopted repeatedly, with abdominal straining, but without defaecation or urination, in female *P. poliocephalus* and *P. alecto* recovering from midline laparotomy (abdominal surgery). Kunz *et al.* also noted that *P. rodricensis* takes this posture for defaecation and urination, but that the helper bat did neither. The helper-mother sequence thus remains an intriguing phenomenon.

Actual parturition occurred with the mother in what Kunz *et al.* describe as a "cradle position", namely suspended quadrupedally by hind-limb and thumb claws, ventral-side up. Kunz *et al.* noted that the birth was "unorthodox" in that it was a breech, whereas most *Pteropus* births are head first, and that the mother,

"probably experienced difficulty during parturition".

They also noted that,

"female *P. rodricensis* and other bat species may assume head-down roosting or "cradle" postures . . . or they may hang upside-down from thumb claws . . . (Wimsatt 1960; West and Redshaw 1987). *The latter posture appears most common*" (my italics).

This last statement does not derive from West and Redshaw (1987), who described emergence of the young as occurring when,

"most mothers . . . adopt a horizontal posture with the ventral surface uppermost", (i.e., in Kunz *et al.*'s "cradle position").

— but from a misinterpretation of Wimsatt's excellent summary.

Wimsatt (1960) dealt with his own observations on *Myotis lucifugus* and a further 15 accounts in which,

> "parturition has been described in greater or lesser detail".

These included two unknown species; eight vespertilionids from five genera; two phyllostomids from two genera; one pteropodid, one rhinolophid and one molossid. I quote Wimsatt's account at length to avoid misunderstanding.

> "In most . . . species . . . the female just before . . . parturition assumes a characteristic posture . . . until parturition is completed . . . If hanging on a vertical surface, the bat reverses . . . and suspends herself head upward, clutching the wall . . . with the claws of the thumbs and feet, and usually with the hind limbs rather widely spread. At the same time the tail is strongly recurved ventrally so that the uropatagial membrane . . . forms a pouch-like receptacle into which the . . . young is . . . received . . . On the other hand, if the female is hanging from a horizontal surface . . . complete reversal of position is not possible . . . the female bends upward and grasps the surface by the thumbs so that she again effects four-way suspension . . . the legs are widely spread and the tail strongly recurved ventrally so that the uropatagium in conjunction with the plagiopatagium and trunk forms a commodious basket into which the newborn can be safely received".

Wimsatt noted that breech-presentation of the fetus occurred in vespertilionid births, and qualified the passage quoted above with,

> "It is probably significant that all bats in which the foregoing posture have been observed . . . are vespertilionids"

and noted that,

> "In . . . *Cynopterus s. sphinx* (Pteropidae) birth was accomplished while the females were hanging from the tops of their cages head downward in the normal resting position, the only concession to the process underway being a wider spreading of the legs than is normal . . . in each case the foetus was delivered head first".

This description, based on Ramakrishna (1950), is entirely consistent with the posture that we observe routinely in parturient *Pteropus*, and has been confirmed by Dr L. S. Hall (pers. comm.), who observed a birth in a captive *Cynopterus*, with the foetus presenting head-first and the mother hanging by the hind-limbs.

I was concerned therefore, by a brief report of the Kunz *et al.* (1994) *Pteropus rodricensis* paper by an unknown author (R.S. 1995) which stated that,

> "the mother-to-be initially assumed the feet-down birthing position, which is *normal in other pteropodid bats* . . . a few times during the birth she shifted to a horizontal "cradle" position or a head-down roosting position, and would only assume *the conventional birthing position* after the helper had demonstrated *the correct way* in front of her" (my italics).

Please note that, from this report, "feet-down" is "normal in other pteropodid bats", (not just *Pteropus*!), and is, moreover, "the conventional birthing position" and "the correct way". My problem with this report is that, my own observations of births in Australian flying-foxes indicate that they follow the pattern described originally for *P. poliocephalus* by Nelson (1965), as a head-first presentation of the foetus, with the mother hanging head down, namely,

> "during parturition the female hangs by the feet and sometimes by a thumb claw too".

A NATURAL RESTING-PHASE DURING PARTURITION IN *PTEROPUS*

Nelson's decription fits most if not all *Pteropus* births that my colleagues and I have seen, including births in *P. scapulatus* (O'Brien, Nankervis and Martin 1996) and a number of *P. poliocephalus* births filmed to illustrate the phenomenon of "punctuated parturition".

This term was coined by Graydon (in an unpublished manuscript describing the **head-down** birthing behaviour of *Pteropus*) for a phenomenon wherein the process of parturition may apparently halt for a considerable period **after** the neonatal head appears. This too was mentioned in Nelson's (1965) description of the complete birth process as,

> "expulsion of the foetus continues smoothly until all of the head is out of the vaginal opening, and then there is a brief pause of 10 minutes or longer".

Nelson also described the *in situ* neonate "head" as having eyes open and showing limited signs of responding to external stimuli. However, Martin, Towers, McGuckin, Little, Luckhoff and Blackshaw (1987)

described pauses of several hours, during which the neonate head turned with eyes open,

> "sometimes vocalising in response to cries of adults",

and cited unpublished observations by Jan Aldenhoven and Glenn Carruthers, of 40 apparently normal births in the wild, in which pauses averaged 50 minutes and varied from about 10 minutes to more than 7 hours (Aldenhoven and Carruthers filmed the flying-fox sequences for the 1985 ABC series, *The Nature of Australia*).

I cannot give an exact figure for the frequency with which "punctuated parturition" occurs in the wild, or indeed in our captive colonies, and one colleague, H. Luckhoff (pers. comm.) who has observed several dozen flying fox births has not seen any with a noticeable pause. Nevertheless, they have been common among our captives, and have never been associated with any obvious neonatal abnormality, or failure of the mother to keep or rear the young to independence.

My most recent observation of a *P. poliocephalus* "punctuated parturition" was in February 1996 — a late birth resulting from late placement of the mother with males. The neonate head was out and dry when technician Anthony had arrived at 0900. It was still out and dry, with mother placid and unruffled, when I arrived at about 1000 (there are, as yet, no records of the head going back in). I monitored the mother at about 20 minute intervals to find youngster wholly out, on the nipple, with cord still attached but placenta undelivered, just before 12.30.

This episode epitomizes my observations of many normal *Pteropus* births: mother calm and head down, neonate head out, a variable quiescent pause of up to several hours, followed by rapid completion of parturition with expulsion of all the sharp and complicated neonatal bits, like wings and claws, in a remarkably short time, a sort of — "whoops, there she goes", or to quote the original full-Nelson (1965),

> "Then with a violent contraction, the shoulders and the rest of the foetus are forced out of the vagina".

It probably does help that the pelvic girdle is "open" in female *Pteropus* to the extent that, ventrally, the pubic bones are separated by a gap of about 2 cm in non-pregnant adults, including one nulliparous bat (Chapman, Hall and Bennett 1994). The gap is closed by an elastic pubic ligament (Martin, unpubl. obs.). Chapman *et al.* (1994) suggest that the reduced reliance of *Pteropus* on hindlimb locomotion, and a diminished hindlimb musculature with less need for muscle attachment to the ventral pubis, has allowed the pelvic girdle to undergo a drastic reduction. They note that loss of this element in females would facilitate the birth of large well-developed young.

DISCUSSION

Now, why such prolixity apropos *Pteropus* parturition and its punctuation? I was dismayed by the inaccurate citing of the literature, and wished to correct the record. I was surprised recently to find an experienced *Pteropus* carer who was unaware of "punctuated parturition" to the extent that, after a neonate head had been "out" for a couple of hours without apparent progress (or maternal distress), took mother to the vet. Fortunately, mother decided that intervention was unnecessary and proceeded apace. But, had she not — what would the vet have done?

As a physiologist I remain intrigued (amazed even) by punctuated parturition — and wish to bring it to the attention of experts in mammalian parturition, and to veterinary surgeons helping flying-fox carer groups. In many (most?) "conventional" species, the birth process, once precipitated, proceeds uninterrupted to completion — unless something is amiss. To be fair to the person seeking veterinary advice, parturition in flying-foxes is an extraordinary phenomenon compared to that in the human, where a long delay after emergence of the head would be classed as severe dystocia (uterine disfunction) and intervention rapidly implemented — forceps, suction, caesarean section?

However, my colleague L. Little (pers. comm.) who has seen "punctuated parturition" many times in our captive flying foxes (and having read the above, in draft) wonders if it is so amazing. She makes the point that, in women, labour is long, but once the infant's head is out, delivery is completed rapidly. On the basis of the human process and her own observations on "assorted ungulates", Little suggests that pauses in delivery, "of a few minutes to hours", are associated with passage of the "difficult parts", the widest parts, usually the shoulders, sometimes the hips. Little describes: an 8 h pause in an "old brood zebra"; a bison, with neonatal head and forelegs out for over an hour, which pulled everything back in and

started again an hour later; a springbok disturbed in labour when the bag was showing through the vulva, stopping labour and resuming it three days later. This last example is believed to be an anti-predator tactic and one which wildebeest also utilize. Little argues that the pause in flying foxes, after emergence of the head, is to allow organisation of the widest/largest and most awkward parts, namely to line up the shoulders, forearms and thumbs, for easy passage through the birth canal.

In utero, the pre-partum foetus is neatly and compactly packaged within the foetal membranes, and is often aligned transversely across the abdominal cavity (Fig. 1). I do not know when, relative to parturition, the foetal head lines up with the birth canal, but suspect that it does not occur until shortly before the onset of parturition. *In utero,* the foetal hind limbs are folded medially against the ventral body surface. The forelimbs are folded more laterally, but still close to the ventral body surface, with the thumbs placed across the shoulders or across the head (Figs 1 and 2). The wing finger bones appear to be bundled parallel with and ventral to the forearms. In dorsal view, the shoulders appear to be the widest part of the foetus (Fig. 2) and this is consistent with Little's thesis.

However, it also seems that the shoulders and wing bones are appropriately positioned well before parturition, so I am not convinced of the need for a period to "line them up". Also, the limbs joints of the neonate appear to be remarkably loose, almost disarticulate, so that, if a limb were wrongly positioned it might well be sufficiently flexible to pass through the birth canal at an odd angle without major damage ensuing. Careful observation of the neonate-expulsion stage is needed to determine how the fore-limbs are arranged during this stage.

It is generally accepted that the overall duration of pregnancy is determined by the foetus. In experiments with domestic animals, where mothers have borne foetuses of different genetic strains, gestation length is that of the foetal strain not the maternal. On the other hand, it is accepted that it is largely mother that determines the time of day at which parturition occurs. In flying-foxes, parturition usually occurs in daytime when the female is in the roost. In any mammal, the foetus is entirely dependent on the placenta for oxygen, and premature separation of the placenta will immediately compromise foetal respiration. Part of the normal process of parturition involves the complex switching of physiological controls from foetal respiration via placenta and umbilical cord, to neonatal respiration via the lungs. In flying-foxes, there is considerable invasion of maternal uterine tissues by the placenta and, its premature separation from

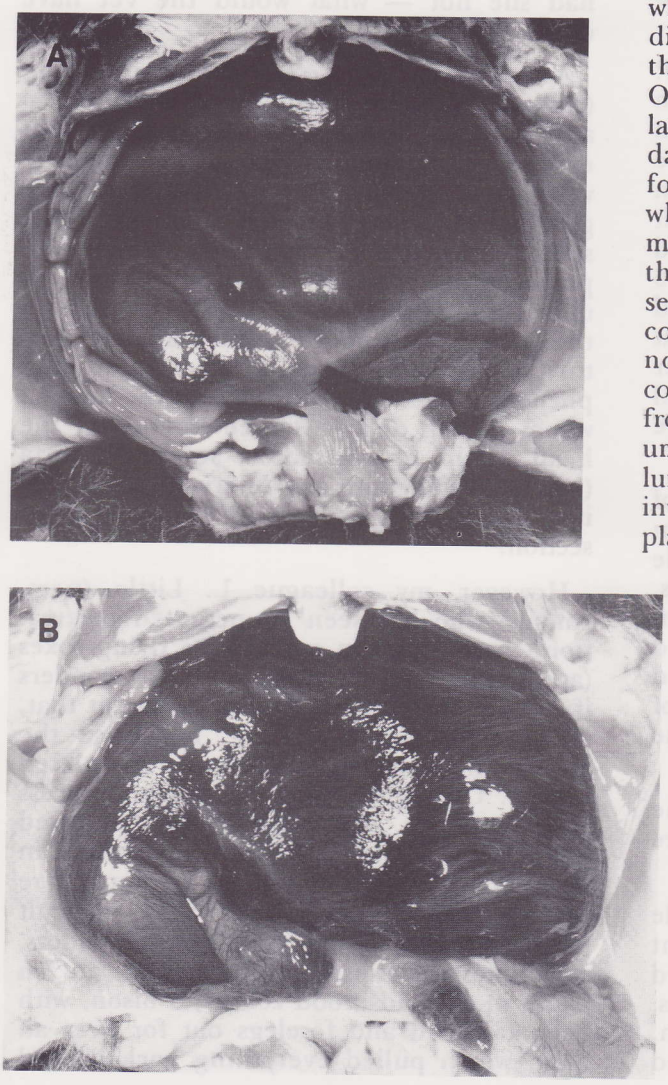

Figure 1. Ventral views of the dissection of a near-term pregnant *P. poliocephalus.*

a) Showing a foetus, enclosed within the left uterine horn; the foetus is aligned transversely and occupies most of the abdominal cavity. The maternal sternum and rib-cage are at the top of the figure; pelvic tissues have been dissected to expose the vagina; the foetal head is visible at the lower left and the placenta at the lower right.

b) The same foetus as in (a) but with uterine and foetal membranes removed and placenta folded back (lower right). The head is folded ventrally, a thumb claw lies across the shoulder and the hind limbs are folded ventrally and cranially.

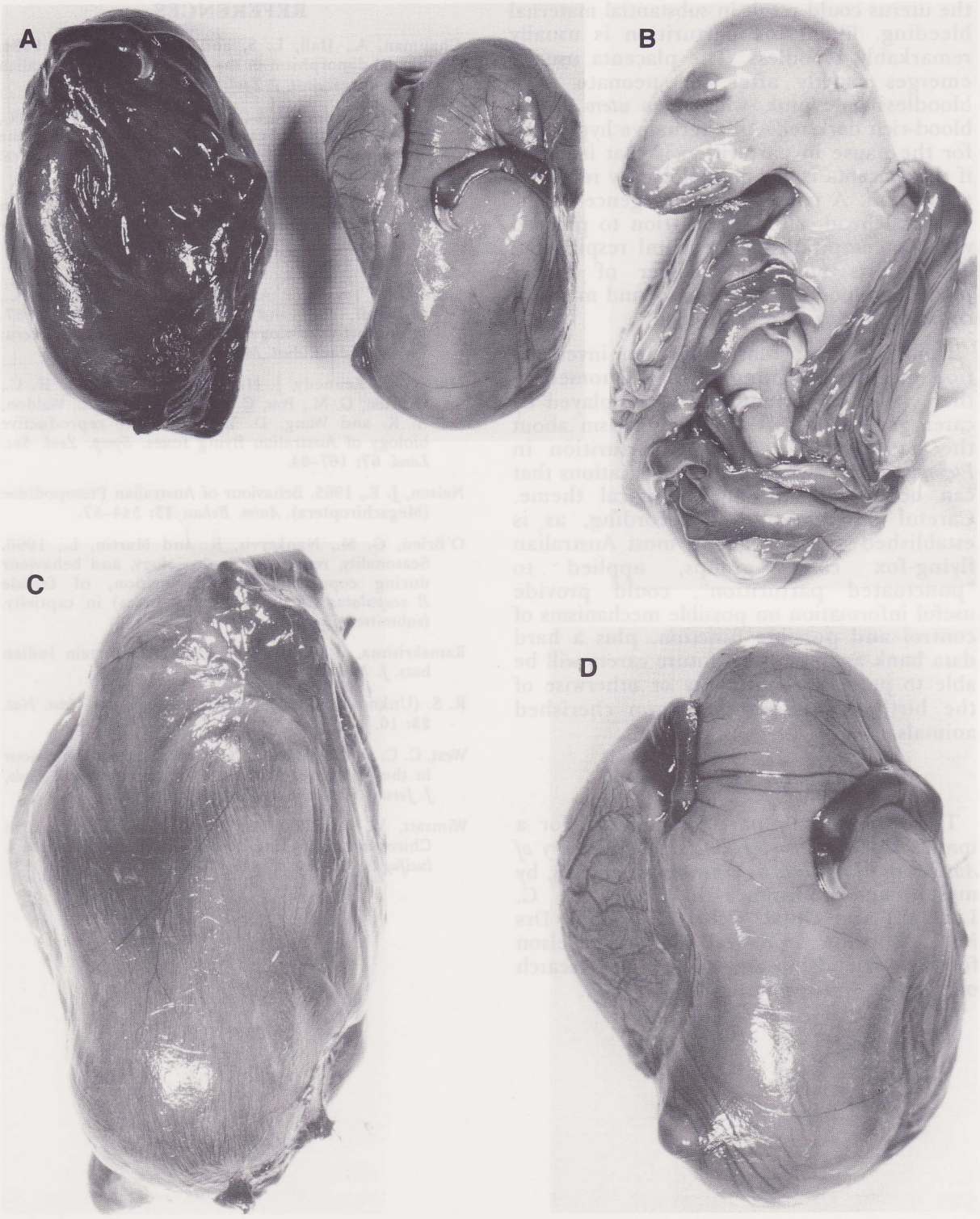

Figure 2. Views of twin *P. poliocephalus* foetuses aborted by a badly injured mother taken into care in Brisbane on 19 September, 1996: foetal and placental weights and forearm lengths for the larger and smaller foetus were respectively, 55.2 g, 7.1 g and 46 mm, and 40.4 g, 7.8 g and 35 mm.

a) General view of the two foetuses; the larger is still mostly enclosed within the foetal membranes. A thumb claw is visible across the shoulder of the smaller foetus and across the head of the larger.

b) Ventral view of smaller foetus showing folding of fore- and hind-limbs.

c) Dorsal view of larger foetus; the right fore-arm is visible, folded close to the torso with the thumb claw close to the head at the top right. The shoulders are clearly the broadest part.

d) Dorsal view of smaller foetus; the thumbs lie across the shoulders. Again, the shoulders are clearly the broadest part of the foetus.

the uterus could result in substantial maternal bleeding. Flying-fox parturition is usually remarkably bloodless. The placenta usually emerges shortly after the neonate as a bloodless pale pink, whereas *in utero* it is a blood-rich dark red. An alternative hypothesis for the pause in parturition is that it occurs if the placenta is not physiologically ready for separation. A pause, *after* emergence of the neonatal head, allows separation to proceed without compromising neonatal respiration, and allows maximal transfer of foetal-placental blood to the neonate, and maximal conservation of maternal blood.

I am convinced that, in further investigation of this intriguing birth phenomenon, there is an important role to be played by carer groups. Despite my dogmatism about the nature and course of parturition in *Pteropus*, I am aware of all the variations that can be played on any biological theme. Careful observation and recording, as is established practice among most Australian flying-fox carer groups, applied to "punctuated parturition", could provide useful information on possible mechanisms of control and possible function, plus a hard data bank against which future carers will be able to judge the normality or otherwise of the birth process in their own cherished animals.

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